Tropical forests and global change: filling knowledge gaps

Pieter A. Zuidema[1], Patrick J. Baker[2], Peter Groenendijk[1], Peter Schippers[1], Peter van der Sleen[1], Mart Vlam[1], and Frank Sterck[1]

[1] Forest Ecology and Forest Management Group, Wageningen University, PO Box 47, 6700 AA Wageningen, The Netherlands
[2] Department of Forest and Ecosystem Science, University of Melbourne, 500 Yarra Boulevard, Richmond VIC 3121, Australia

Tropical forests will experience major changes in environmental conditions this century. Understanding their responses to such changes is crucial to predicting global carbon cycling. Important knowledge gaps exist: the causes of recent changes in tropical forest dynamics remain unclear and the responses of entire tropical trees to environmental changes are poorly understood. In this Opinion article, we argue that filling these knowledge gaps requires a new research strategy, one that focuses on trees instead of leaves or communities, on long-term instead of short-term changes, and on understanding mechanisms instead of documenting changes. We propose the use of tree-ring analyses, stable-isotope analyses, manipulative field experiments, and well-validated simulation models to improve predictions of forest responses to global change.

Changing biomass in tropical forests

Tropical forests cover just 7% of the Earth's land surface but store 25% of global terrestrial carbon and account for one- third of net primary productivity [1]. Because tropical forests are so rich in carbon, their net loss or uptake of carbon has important implications for atmospheric CO_2 levels [2]. Past increases in atmospheric CO_2 levels, increased nutrient deposition and climatic changes are likely to have affected tree growth and forest dynamics. Understanding the accumulated impacts of these changes – which we term 'global-change factors' – is crucial for predicting future dynamics of tropical forests and for informing adaptation policies [3]. Here we focus on the effects of changing climate and nutrient availability on relatively undisturbed tropical forests, leaving out the direct effects of other anthropogenic disturbances (exploitation) [4].

There is a growing body of empirical evidence for changing biomass (and carbon) in relatively undisturbed tropical forests over the past few decades. A range of studies in permanent sample plots (see Glossary) located in intact tropical forests have reported increasing biomass [2,5] and tree growth rates [6] over the past decades. Other studies have found that tree growth rates decreased [7] or fluctuated over time [8,9]. Although these studies have established the foundation for reporting changes in tropical forest dynamics, permanent plot data are not well suited – and have so far failed – to identify the causes of the observed biomass changes [10] (see [11] for an exception). Permanent-plot studies do not allow separation of the effects of different global change factors [11] and offer limited possibilities to relate biomass (or tree growth) changes to climatic variation because they are usually remeasured after approximately 5 years. As a result, suggested causes for the changing dynamics in undisturbed tropical forests still range from shifts in climatic and atmospheric conditions (CO_2, rainfall, temperature) to increased nutrient deposition and recovery after major disturbances [2,5]. This poor understanding of the effects of global change on tropical forests is worrying because it hampers our ability to forecast forest responses, estimate the probability of tropical forest dieback, and develop effective adaptation strategies to future global changes [3].

In this Opinion article, we posit that major advances in the field can be achieved with new research approaches. We first briefly discuss knowledge gaps in the field, drawing on recently published reviews [2–4,10–13] to show that knowledge gaps primarily relate to poor understanding of tree- and population-level responses to global changes. We then suggest that filling these knowledge gaps requires a different research strategy, one that focuses on trees instead of leaves or entire forest stands, considers long-term

Glossary

Individual-based models: a specific type of population model in which the growth, survival, and reproduction of each individual are simulated over time in response to its environment.

Intrinsic water-use efficiency (iWUE): the ratio of net CO_2 assimilation to stomatal conductance.

Isotopomer: a molecule carrying a heavy isotope in a particular group.

Mechanistic tree-growth models: software tools that use knowledge on physiological processes in trees and tree responses to environmental conditions to simulate tree growth over time.

Permanent sample plots: areas of forest – usually 1–50 ha in size – where all trees above a certain minimum size are tagged and mapped and their diameter and status (alive, dead, newly recruited) is recorded repeatedly (every 1–5 years).

Population models: software tools that predict the development of natural populations of trees (or other species) in time, based on information on growth, survival, and reproduction.

Species-range modeling: the simulation of (changes in) the geographic distribution of species in response to (changes in) climate.

Stable-isotope analyses: chemical analyses to determine the fraction of stable isotopes in plant materials. Stable isotopes are variations of an element that differ in the number of neutrons in the nucleus and as a result have different physical and chemical properties (Box 2).

Corresponding author: Zuidema, P.A. (Pieter.Zuidema@wur.nl)
Keywords: tropical forests; climate change; tree-ring analysis; stable isotopes; tree-growth models; manipulative field experiments.

1360-1385/$ – see front matter
 http://dx.doi.org/10.1016/j.tplants.2013.05.006

instead of short-term changes, and focuses on understanding mechanisms instead of describing patterns and documenting changes. We argue that four research approaches that are rarely used in tropical forests have the potential to help fill these knowledge gaps: (i) tree-ring analyses; (ii) stable-isotope analyses; (iii) well-validated mechanistic simulation models; and (iv) large-scale manipulative experiments. We introduce and discuss these approaches and make a plea to integrate existing and proposed research approaches to accelerate developments in this field.

Gaps in knowledge

Leaf and tree level

Major advances in the field of the climate sensitivity of forest trees have been achieved in experimental studies of leaf-level physiological responses (photosynthesis, respiration) to changing environmental conditions (reviewed in [14,15]). Overall, there is good theoretical and empirical understanding of how rates of leaf photosynthesis respond to changes in CO_2 level, temperature, and availability of nutrients and water (Figure 1). It is, however, desirable to study responses to integrated effects of warming and CO_2 enrichment in the field, on leaves attached to trees, and for a larger set of species.

By contrast, understanding of environmental changes at the level of mature trees is limited (Figure 1). The fate of carbon in trees is poorly understood and this greatly limits our ability to predict how climate-induced changes in leaf photosynthesis and respiration influence growth in woody biomass [16]. Plot and tree-ring studies have reported reduced diameter growth during low-rainfall and high-temperature years [8,9,17], but hardly anything is known about the effects of gradual climatic changes. Manipulative experiments in which global change factors have been altered are rare. Nutrient addition studies (N + K) have reported stimulation of diameter growth for small trees [18] and experimental drought studies have reported strong reductions in tree growth and survival [19]. So far, the effects of either CO_2 increase or warming have been experimentally tested only for tropical seedlings (and tree leaves [20] or branches [21]). Seedling studies showed declining biomass growth with increasing temperature [22] and growth stimulation after CO_2 enrichment [12]. Although these studies provide insights into climate-change effects on a crucial stage in a

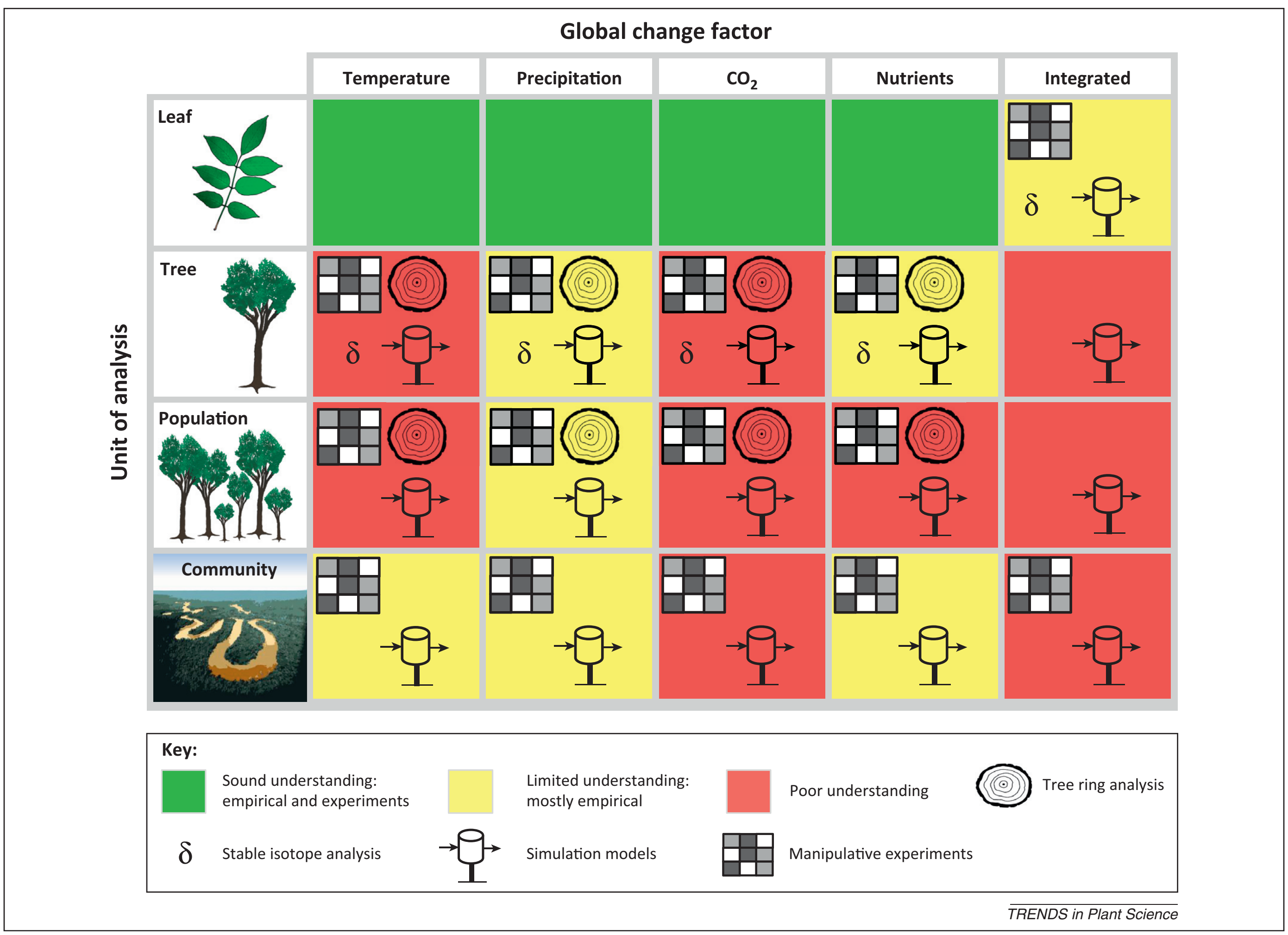

Figure 1. Knowledge gaps and new research approaches in the field of global-change impacts on tropical forests. Colors indicate our level of understanding of the responses of leaves, individual trees, tree populations, and forest communities to four global-change factors and their integrated effect. Symbols in colored cells indicate proposed research approaches to fill knowledge gaps. Tree-ring analysis: climate-growth relations and detecting long-term growth changes. Stable-isotope analysis: ^{13}C, ^{18}O, and ^{15}N from tree rings. Simulation models: mechanistic tree-growth models, population models, and community-level models. Manipulative experiments: free-air CO_2 enrichment (FACE), warming, and changing water availability. Population and community level are typically at the 10–500 ha scale. Note that changes in light levels (i.e., global dimming/brightening or changes in cloud cover) were not included in this scheme.